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## PROPORTIONS AND ALLOMETRY IN THE GRAY SQUIRREL, *SCIURUS CAROLINENSIS*

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### INTRODUCTION

The anatomy of *Sciurus* has been treated in part by many authors. Cranial anatomy has been studied in some detail, notably by Olson and Miller (1958), Guthrie (1963), and in some papers on sciurid taxonomy. Postcranial anatomy has been treated more superficially. Owen (1866) and Flower (1885) included a few descriptions of sciurid osteology; Parsons (1894) described the myology of *Sciurus prevosti*; Peterka (1936) listed some osteologic and myologic aspects of the anatomy of *Sciurus niger*; and several authors have used postcranial anatomy to determine age in *Sciurus carolinensis* (Kirkpatrick and Barnett, 1957). However, there is no adequate description of the proportions of any species of *Sciurus*. There are data on the commonly recorded external measurements (total length, tail length, length of hind foot, and height of ear), but these provide a poor description of body proportions and are completely inadequate for comparisons of locomotor anatomy. Therefore, one of the objectives of this paper is to provide a description of the proportions of one species of *Sciurus*, that it may serve as a basis for comparisons with other mammals.

In contrast, the primate literature is full of measurements of body proportions of prosimians, monkeys, and apes (see particularly Schultz, 1930, 1933, 1937, 1938, 1953; Erikson, 1963; and data summarized in Napier and Napier, 1967, pp. 393-395). However, the lack of comparative data from nonprimate mammals presents a significant problem. It inevitably leads to a lack of perspective, particularly a lack of appreciation of the different ways in which nonprimates have overcome the same locomotor problems faced by primates. Primarily to highlight this factor and because of the extent of our knowledge of primate proportions, the data in this paper are compared in detail with those of Erikson (1963). The obvious comparison to be made is between squirrels and marmosets, which live and move about in similar ways. One might

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hypothesize that the proportions of gray squirrels would approximate those of marmosets, tamarins, and other ceboids included in Erikson's springer group. This hypothesis will be evaluated later.

A more general objective of this paper is to consider the appropriateness of using ratios to compare animals of different sizes. Kowalski (1972) has wisely remarked on the desirability of using ratios if they behave in a simple way. However, it seems evident from published data that ratios frequently do not behave simply. Since this problem is basic to describing shape, it was examined in detail in each analysis.

Finally, the subject of robustness is reexamined with data from *Sciurus*. Usually robustness is defined in terms of lengths and distal widths of the humerus and femur (Jolicoeur, 1963; Goldstein, 1972). The objective of this reexamination is simply to evaluate the appropriateness of using distal widths of limb bones as general measures of robustness.

### Acknowledgments

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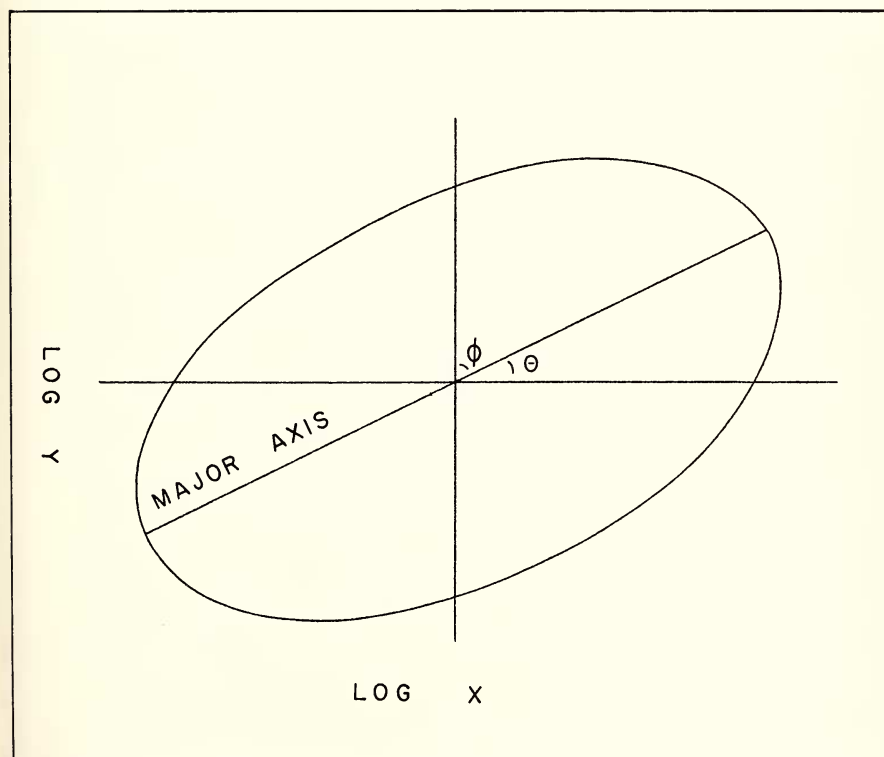
### MATERIALS AND METHODS

The 67 squirrel skeletons measured for this study include 27 from eastern Massachusetts (personal collection), 26 from the Delmarva Peninsula (Delaware Museum of Natural History), and 14 from the vicinity of the District of Columbia and other nearby eastern localities (in the U.S. National Museum).

The measurements of vertebrae and long bones are based on the discussion and warnings of Erikson (1963), who in turn based his measurements on Schultz (1929). Femur length was measured from the

femoral head to the medial condyle. In *Sciurus* this differs very little from Schultz's measurement, taken from the greater trochanter to lateral condyle. Lengths of other long bones are greatest lengths. Vertebral lengths were taken ventrally on dried, straightened vertebral columns. The length of the cervical vertebrae is measured from the anterior end of the odontoid process of the axis to the posterior end of the centrum of C7. In squirrels the trunk length, as measured by the sum of the lengths of thoracic, lumbar, and sacral vertebrae, is slightly less than the suprasternal to symphysis length, taken by Schultz and others as a measure of trunk length.

For a study of robustness of long bones, seven measurements of bone widths were taken and compared with the lengths of the respective bones. These were the greatest width across the tubercles of the humeral head, the least width at the middle of the humerus, the maximum epicondylar width at the distal end of the humerus, the greatest



**Figure 1:** Definition of the major axis by directional cosines. A value  $z$  on the major axis is defined by  $z = \cos \theta \log x + \cos \phi \log y$ . The major axis is the allometric equation  $y = bx^a$ , in which  $a = \cos \phi / \cos \theta$ . The isometry hypothesis is  $\cos \theta = \cos \phi$ .

and least widths at the middle of the femur, the greatest width of the femoral condyles, and the least width of the tibia. The middles of the humerus and femur were estimated with a millimeter rule and marked before the respective widths were measured. Jolicoeur (1963) and Goldstein (1972) used only distal widths—the maximum epicondylar width of the humerus and the greatest width of the femoral condyles. The other measurements used in this study were chosen to provide measures of the robustness of the proximal end and midshaft of the bones.

Analysis of the proportions is based on the discussion of the multivariate solution of the allometric equation presented by Jolicoeur (1963). It utilizes principal component analysis based on the variance-covariance matrix of logarithmically transformed data. In this procedure the major axis of the ellipsoid of data points is determined, an axis which accounts for the most variance and is the best description of the allometric relationship between the variables. In principal component analysis this axis is defined by a series of factors, which are weightings of the original variables. In Q mode, each factor is the cosine of the angle formed by the major axis and a line through the centroid parallel to the axis of its respective variable. For two dimensions this is illustrated in Figure 1. If there is an isometric relationship between variables, all the cosines are the same. With two variables the major axis meets the  $x$  and the  $y$  axes at  $45^\circ$  angles and the two cosines are both 0.707. With three variables the angles are  $54.7^\circ$  and the cosines are 0.577.

The cosines are easily computed for four or more variables, although visualization of this situation becomes difficult. The isometry hypothesis is represented by the vector with all cosines equal. The angle between the observed major axis and this (or any other) hypothesized vector can be determined from their dot product. Anderson (1963) and Jolicoeur (1963) present and discuss a test of significance of the difference between an hypothesized vector and the observed vector. If the observed vector differs significantly from the isometric vector, one must conclude that the data demonstrate a size-related change in shape.

The standard bivariate allometry equation can easily be derived from the multivariate solution. For any two variables the constant of allometry (i.e., the exponent of the equation) can be determined by dividing the cosine of one variable by the cosine of the other. The other constant of the equation can be obtained by substituting mean values of the two variables in the equation.

An extension of Jolicoeur's procedures is desirable because isometric relationships between variables do not preclude size-related changes in shape. If the relationships do not differ significantly from isometry, the untransformed data should be analyzed. Again, a principal component analysis will yield the major axis of the ellipsoid of original data

points (again in Q mode). The ratios between the variables will remain constant only if the major axis has the same direction as the line connecting the origin and the centroid of the ellipse—this line is the mean vector—as is the case when the  $x$ ,  $y$ , and other intercepts are all zero. Therefore, the test of constant proportions (e.g.,  $y/x = k$ ) is provided by the null hypothesis that the major axis does not differ in direction from the mean vector (see Figure 2). The cosines are easily calculated for the angles between the mean vector and the axes of the variables. The angle between the major axis and the mean vector may be determined from the dot product of the vectors divided by the product of their lengths, and the significance of this divergence may be determined as described by Jolicoeur. Again, if there is a significant difference, then the data demonstrate that proportions change with size.

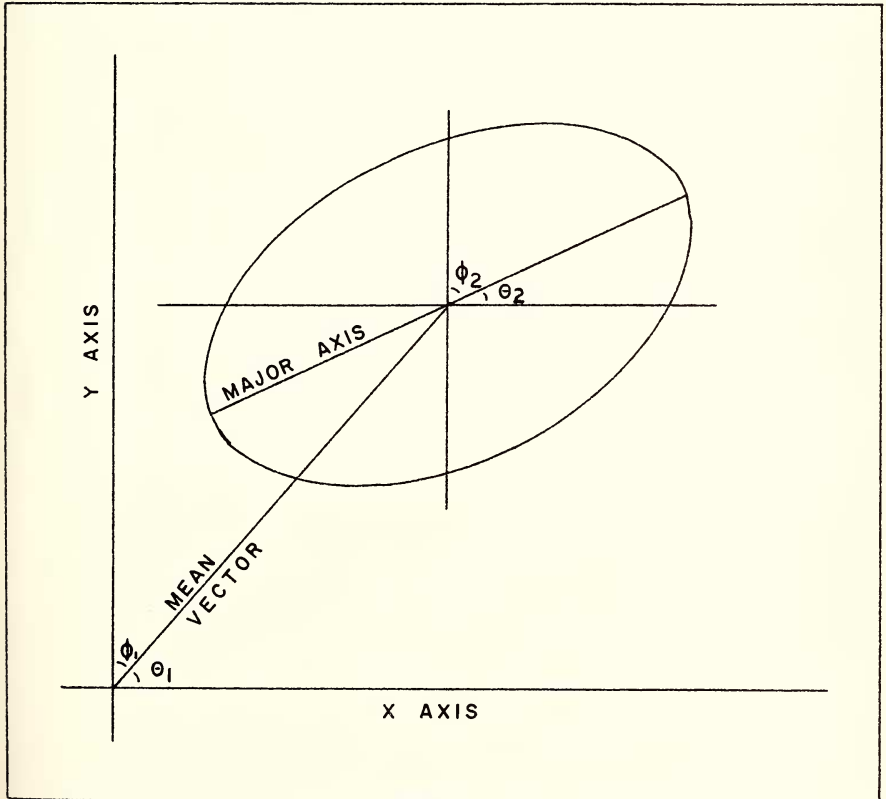


Figure 2: Test of constant ratio between untransformed variables. Ratios are unaffected by size, e.g.,  $y/x = k$ , if  $\theta_1 = \theta_2$  and  $\phi_1 = \phi_2$ .

## GENERAL DESCRIPTION

Most gray squirrels examined had seven sternebrae and 26 presacral vertebrae. The first seven vertebrae were cervical, the next 12 were rib-bearing (the classic thoracic vertebrae), and the last seven were lumbar vertebrae. The tenth thoracic vertebra was the anticlinal vertebra. It and the posterior vertebrae had a lumbar type of articulation (Washburn and Buettner-Janusch, 1952). Thus, as defined by articulations there were 10 thoracic and nine lumbar vertebrae. There were three sacral vertebrae and 26 to 29 caudal vertebrae. The normal and variant vertebral formulae of 51 skeletons are presented in Table 1.

In the quantitative analyses of proportions, only the normal animals were used. This avoided the use of data that are not strictly comparable. Similarly, specimens with pathological conditions were not included. Three animals (of 65 carefully examined) exhibited broken bones which were healing: one fractured humerus, two fractured femora, and one fracture of both tibia and fibula. There was one case of bilateral aplasia of the neck of the femur. In this skeleton the humeri were abnormally thick and short; it was similarly excluded from these analyses.

The sample was treated as a whole and was not subdivided by sex, age, or geographic origin of the specimens unless indicated. All specimens were aged by degree of closure of epiphyseal sutures of humeri and femora, as described by Kirkpatrick and Barnett (1957). Adults were defined as animals with complete fusion of the diaphysis and distal epiphysis of the femur. There was considerable overlap in size between juvenile animals and adults, as will always be true when the adults are defined by closure of growth sutures. However, the overlap was greater in this sample because of the geographic heterogeneity of the sample. Only eight juveniles had shorter femora than that of the smallest adult. Among the 25 adult animals, the average animal from Massachusetts had a longer femur than the average squirrel from Delaware and Maryland.

## RESULTS

The body proportions of *Sciurus carolinensis* are summarized in Figure 3. Limb proportions are presented proportional to a trunk length of 100 units. In Tables 2 and 3 the data are presented as indices (the ratios are multiplied by 100) and compared with the indices reported by Erikson (1963) for different kinds of neotropical primates. He divided ceboids into three locomotor types: springers, climbers, and brachiators. With respect to relative lengths of forelimb to trunk and of forelimb to hindlimb, gray squirrels appear to be "superspringers."

**Table 1: Normal and Unusual Vertebral Patterns in *Sciurus carolinensis***

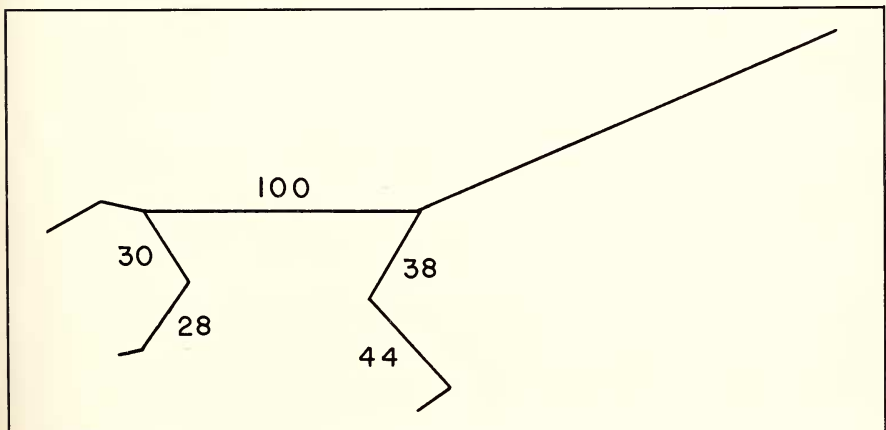
	CERVICAL	THORACIC	LUMBAR	SACRAL
Normal (N = 45)	7	12	7	3
RWT 1149 ♀	7	12	8	2
RWT 1148 ♂	7	12½	7½	3
DMNH 4212 ♂	7	12	7	2
DMNH 4211 ♀	7	13	6	3
USNM 248247 ♀	7	12	7	4
DMNH 2968 ♀	7	12	7	4

**Table 2: Relative Lengths<sup>1</sup> of Long Bones for *Sciurus carolinensis* and Ceboid Primates<sup>2</sup>**

	SQUIRRELS		CEBOID PRIMATES	
	<i>Sciurus</i>	Springers	Climbers	Brachiators
Hum. + Rad. Vert. Col.	58	67	84	123
Hum. + Rad. Fem. + Tib.	71	75	80	101
Radius Humerus	96	89	90	94

<sup>1</sup> Data presented as indices (ratios multiplied by 100).

<sup>2</sup> Data from Erikson, 1963.

**Figure 3: Body proportions of *Sciurus carolinensis*.**

**Table 3: Relative Lengths<sup>1</sup> of Lumbar and Thoracic Vertebrae for *Sciurus carolinensis* and Ceboid Primates<sup>2</sup>**

	SQUIRRELS		CEBOID PRIMATES	
	<i>Sciurus</i>	Springers	Climbers	Brachiators
Lumb. Length* Thor. Length*	97	110	91	57
Lumb. Length† Thor. Length†	148	195	167	96

<sup>1</sup> Data presented as indices (ratios multiplied by 100).

<sup>2</sup> Data from Erikson, 1963.

\* Defined by ribs.

† Defined by articulations.

With respect to their brachial index, however, they appear anomalously to be similar to the neotropical brachiators. With respect to relative lengths of lumbar and thoracic parts of the vertebral column, whether defined by their ribs or by their articulations, gray squirrels are similar to Erikson's climbers.

In order to obtain a better understanding of the proportions of gray squirrels and how they might be expected to change with changes in size, a more detailed analysis of the linear measurements was undertaken. These analyses are described in the section on methods, to which the reader is referred before examining the results presented in the following section.

### Lengths of Vertebrae

The lengths of six segments of the vertebral column are presented in Table 4. The principal component analysis (Table 5) conducted on the log-transformed data demonstrates that these are not isometric. The most divergent measurement is the length of the sacral vertebrae, which accounts for most of the  $X^2$  value. The serial decline in the directional cosines from cervical to sacral vertebrae suggests an anterior-posterior growth gradient, similar to those described by Huxley (1932) for extremities.

The lengths of thoracic and lumbar vertebrae, which are sometimes used to form ratios, are approximately isometric with respect to each other (Table 6). The untransformed data were examined, and the principal axis was found to diverge from the isometric by  $1.5^\circ$ , mostly in



**Table 4: Lengths and Ratios of Limbs and Vertebral Segments of *Sciurus carolinensis***

	N	MEAN	S.E.	C.V.	SKWENESS <sup>1</sup>	KURTOSIS <sup>2</sup>
<i>Lengths:</i>						
Forelimb (Humerus + Radius)	45	84.44	.54	4.2	-.57	0.2
Hindlimb (Femur + Tibia)	46	118.91	.73	4.1	-.64	0.5
Cervical Vertebrae	46	24.07	.21	5.8	-.47	0.0
Vertebrae T1 to T10	46	49.88	.40	5.4	-.29	0.5
Vertebrae T1 to T12	46	62.66	.48	5.2	-.20	0.3
Vertebrae T11 to L7	46	73.60	.52	4.7	-.41	-0.2
Vertebrae L1 to L7	46	60.78	.44	4.9	-.60	0.0
Sacral Vertebrae	45	21.18	.13	3.9	.29	-0.1
Thoracic, Lumbar, and Sacral Vertebrae	45	144.85	.92	4.2	-.26	0.3
<i>Ratios:</i>						
Brachial (Radius/Humerus)	43	.96	.003	2.1	-.24	-0.5
Crural (Tibia/Femur)	43	1.13	.003	1.8	.35	-0.2
Intermembral (Forelimb/Hindlimb)	43	.71	.001	1.1	.26	1.1
Forelimb/Trunk vertebrae	43	.58	.003	2.9	.54	0.8
Hindlimb/Trunk vertebrae	43	.82	.004	2.8	.29	-0.1
L1 to L7/T1 to T12	43	.97	.004	2.5	.06	-1.0
T11 to L7/T1 to T10	43	1.48	.007	3.2	-.40	0.0

<sup>1</sup> Skewness =  $\Sigma (x - \bar{x})^3 / Ns^3$

<sup>2</sup> Kurtosis =  $\Sigma (x - \bar{x})^4 / Ns^4 - 3$

**Table 5: Demonstration That Vertebral Lengths Are Not Isometric with One Another (N = 46)**

LOG TRANSFORMED LENGTHS:	C1-7	T1-10	T1-12	T11-L7	L1-7	S1-3
Major Axis	.460	.455	.437	.398	.425	.227
Isometry Hypothesis	.408	.408	.408	.408	.408	.408

82.3% of the variance is accounted for by the first principal axis. The null hypothesis that the principal axis is not significantly different from the isometry hypothesis is rejected ( $X^2 = 40.5$   $p < .001$ ). The two axes diverge by 11.5°.

the plane of the T1-10 and T11-L7 axes. The divergence is not significant and suggests that the ratios of these vertebral lengths do not change significantly within the size range of gray squirrels.

**Table 6: Approximate Isometry of Lengths of Thoracic and Lumbar Vertebrae (N = 46)**

LOG TRANSFORMED LENGTHS:	T1-10	T1-12	T11-L7	L1-7
Major Axis	.530	.509	.464	.495
Isometry Hypothesis	.500	.500	.500	.500

The major axis accounts for 89.5% of the variance of the four variables. The isometry hypothesis is not rejected ( $X^2 = 4.3$   $p \cong 25\%$ ). The two axes diverge by 2.5°.

UNTRANSFORMED LENGTHS:	T1-10	T1-12	T11-L7	L1-7
Major Axis	.423	.520	.563	.484
Hypothesis of Constant Ratios	.400	.503	.591	.488

The major axis accounts for 91.5% of the variance of the four variables. The hypothesis of constant ratios is not rejected ( $X^2 = 2.5$   $p \cong 50\%$ ). The two axes diverge by 1.5°.

### Lengths of Limbs

The trunk length (the sum of the lengths of the thoracic, lumbar, and sacral segments) was compared with the limb lengths, where the forelimb length is taken as the sum of lengths of humerus and radius, the hindlimb length as the sum of lengths of femur and tibia. As shown in Figure 3, the forelimb is 58 per cent of the trunk length and the hindlimb is 82 per cent of the trunk length. The principal axis of log-transformed data is shown in Table 7. The observed eigenvector diverges from that of the isometry hypothesis by 5.2°, but the observed values are not significantly isometric ( $X^2 = 0.9$   $p > 50$  percent). Similarly, the major axis of the untransformed variables does not differ significantly from the hypothesis of equal ratios.

The lengths of the long bones are presented in Table 8. The log-transformed data were examined for size allometry, and the results are presented in Table 9. The first eigenvector accounts for 95.5 per cent of the variance, and the vector diverges from the vector of isometry by

**Table 7: Approximate Isometry of Trunk and Limb Lengths (N = 45)**

LOG TRANSFORMED LENGTHS:	FORELIMB	HINDLIMB	TRUNK
Major Axis	.604	.594	.531
Isometry Hypothesis	.576	.576	.576

The major axis accounts for 88% of the variance. The isometry hypothesis is not rejected ( $X^2 = 0.9$   $p > 50\%$ ). The two axes diverge by 5.2°.

**Table 8: Lengths of Long Bones of *Sciurus carolinensis***

	N	MEAN	S.E.	C.V.
Humerus	61	43.02	.25	4.5
Radius	61	41.18	.24	4.5
Femur	61	55.63	.35	4.9
Tibia	61	62.98	.32	4.0

**Table 9: Allometry in the Lengths of Long Bones of *Sciurus carolinensis* (N = 61)**

LOG TRANSFORMED LENGTHS:	HUMERUS	RADIUS	FEMUR	TIBIA
Major Axis	.500	.493	.559	.441
Isometry Hypothesis	.500	.500	.500	.500

The major axis accounts for 95.5% of the total variance. The isometry hypothesis is rejected ( $X^2 = 33.4$   $p < .001$ ). The two axes diverge by  $4.8^\circ$ .

$4.8^\circ$  ( $X^2 = 33.4$   $p < .001$ ). Most of the divergence from isometry is found in the plane of the measurements of the femora and the tibia, indicating that the femora are relatively longer in larger animals and the tibia relatively shorter.

In Table 10 a comparison is made with a similar analysis conducted on a small sample ( $N = 30$ ) of tamarins, *Saguinus oedipus*. The major differences between tamarins and gray squirrels are that the tibia of the tamarins is not negatively allometric, whereas the radius appears to be. The principal axis of the tamarin does not differ significantly from the axis of isometry ( $X^2 = 3.6$   $p > .25$ ). However, the sample size is small so one cannot state with confidence that the measurements are isometric.

**Table 10: A Comparison of Long Bone Measurements of *Sciurus carolinensis* (N = 61) and *Saguinus oedipus* (N = 30)**

		HUMERUS	RADIUS	FEMUR	TIBIA
Major Axes (Log Transf.)	<i>Sciurus</i>	.500	.493	.559	.441
	<i>Saguinus</i>	.499	.450	.531	.517
Mean Vectors	<i>Sciurus</i>	43.02	41.18	55.63	62.98
	<i>Saguinus</i>	51.43	46.48	64.98	66.33
Standardized Mean Vectors	<i>Sciurus</i>	.417	.400	.540	.611
	<i>Saguinus</i>	.444	.401	.561	.572

In a comparison of the standardized mean vectors it is evident that the greatest difference is in the relatively longer tibia of *Sciurus*. Lesser differences are the relatively longer humerus and femur of the *Saguinus*. These data combined with extrapolation of the allometric relationships for *Sciurus* suggest that larger gray squirrels would have a crural index more similar to that of the tamarin than do the ones used in this study. The higher brachial index of *Sciurus* is due to its relatively shorter humerus. Since the humerus and the radius of *Sciurus* have similar directional cosines, the brachial index of this species should be little affected by size. The directional cosines of the humerus and radius of *Saguinus* suggest that the brachial index of this species may be inversely proportional to the size of the animal. A larger sample is necessary to adequately test this hypothesis.

### Robustness of Limbs

The robustness of three of the long bones was examined by principal component analysis, paralleling and extending the studies by Jolicoeur (1963) and Goldstein (1972). A sample of 45, including skeletons of young and adult animals, was studied first. The lengths of the humerus, femur, and tibia were associated with similar values in the first eigenvector. A directional cosine of approximately 0.30 would appear to be associated with length measurements in this analysis. Therefore, a directional cosine of approximately 0.45 should be associated with width measurements, if these increase at the 1.5 power of limb lengths as is usually hypothesized. This value is approximated by the directional cosines of the least width of the humerus at midshaft and the greatest width of the femur at midshaft. Widths of the proximal and distal ends of the humerus and of the distal end of the femur are associated with cosines well below the expected value. In fact, they are negatively allometric to the length measurements. Thus, for this cross-sectional series of growth stages, some widths of the diaphyses increase at approximately the 1.5 power of limb lengths, whereas widths of the epiphyses do not.

To determine whether these results might be peculiar to a growth series, the analysis was repeated on a sample of 24 fully adult skeletons, in which the epiphyses and diaphyses were completely fused. The lengths of the long bones were associated with directional cosines of 0.26 in this analysis. Therefore, widths which increase at the 1.5 power of length should be associated with cosines of approximately 0.39. The greatest and least widths of the femur at midshaft fit this prediction, whereas the distal widths of the humerus and femur are better described

as being approximately isometric with the lengths of these bones. The other widths increase at rates intermediate between 1.0 and the 1.5 power of length. In Table 11 the directional cosines of the two samples are listed together with the approximate ratio of each cosine to that of the length of the humerus. (This ratio is equal to the constant of allometry for each variable compared with the length of the humerus.) This allows easy comparison of the differences between the total sample and the sample of adults only and shows clearly which widths do not increase at the 1.5 power of length.

## DISCUSSION AND CONCLUSIONS

There are several kinds of size allometry which must be distinguished from one another. The one given primary emphasis in this paper is the allometry found in a sample of young to adult animals. It must be distinguished from growth allometry and from the allometric relationships found within or between samples of fully grown animals of different sizes. A basic hypothesis of this paper is that the allometry found is functionally important. In this sample of growing and adult animals, all were out of the nest and facing the same environmental problems of locomotion, feeding, and so on. Therefore, it is reasoned that the functionally important relationships between linear measure-

**Table 11: Size Allometry of Lengths and Widths of Long Bones of *Sciurus carolinensis***

Variable	DIRECTIONAL COSINES OF MAJOR AXIS			
	Total sample (N = 45)	Approx. ratios*	Adults (N = 24)	Approx. ratios*
Humeral Length	.30	1.0	.26	1.0
Width of Humeral Head	.19	0.6	.33	1.3
Least Midshaft Diameter	.48	1.6	.30	1.2
Distal Width	.11	0.4	.23	0.9
Femoral Length	.32	1.1	.26	1.0
Greatest Midshaft Diameter	.45	1.5	.42	1.6
Least Midshaft Diameter	.38	1.3	.40	1.5
Condylar Width	.22	0.7	.30	1.2
Tibial Length	.27	0.9	.26	1.0
Least Tibial Width	.26	0.9	.34	1.3

\* The ratios are equal to  $a$  in the equation  $y = bx^a$ , where  $x$  is the length of the humerus and  $y$  is the other variable listed.

ments are the same or similar to the relationships that would be found in a sample of adults of the same species. Unfortunately the small sample size of adults precludes critical testing of this hypothesis in this study. Examination of the data suggests that it is valid for length measurements of the vertebrae and limb bones, but that it is not valid for comparisons of lengths and widths of the long bones. It is particularly likely to be invalid for widths of epiphyses.

If these allometric or isometric relationships are functionally important, then biological scaling factors (Stahl, 1962) may be derived from them. The multivariate solution of the allometry equation is analogous to such factors. In some instances it may be identical with the relationship described by various ratios of the average lengths; in other cases it is not.

The data on the gray squirrel demonstrate that there is size allometry between different segments of the vertebral column but this does not appear to affect the ratios presented in Table 3. If the ratios for the ceboids are similarly unaffected by absolute size, then this comparison of *Sciurus* and larger ceboids would seem valid. However, the modal number of rib-bearing vertebrae is 13 for both the ceboid springers and climbers, whereas it is 12 for *Sciurus*. If the vertebrae are defined by their articulations, the modal numbers of thoracic and lumbar vertebrae are the same for these ceboids and for gray squirrels. Therefore, the relative proportions of vertebrae are more comparable when that definition is used.

The conclusion is that gray squirrels have a relatively shorter lumbar segment of the vertebral column than do most of the nonbrachiating ceboid monkeys. This is the segment that is flexed and extended when the animal jumps, so the implication is that the monkeys have a vertebral column more adapted to jumping. However, in primates and squirrels the amount of flexion which actually occurs between lumbar vertebrae is much greater in the middle of the back than near the sacrum. In an x-ray examination of a gray squirrel, it appears that most of the ventrodorsal flexion of the vertebral column occurs in the joints between the vertebrae T10 and L2. Therefore, conclusions about the functional significance of the relative length of the whole lumbar segment should be tempered, and other measures of the locomotor significance of the lumbar part of the vertebral column should be sought.

The lengths of the forelimb, hindlimb, and trunk vertebrae (thoracic, lumbar, and sacral) are apparently isometric. The relative shortness of the forelimb of *Sciurus* (shown in Table 2), then, is a real difference between it and ceboids of various sizes.

The lengths of the long bones are significantly allometric, but most of the divergence from isometry occurs in the lengths of the femur and tibia. The lengths of the humerus and radius are approximately isometric to each other; consequently, the high brachial index of *Sciurus carolinensis* (Table 2) would therefore appear to be a noteworthy characteristic. As is demonstrated by the standardized mean vectors, shown in Table 10, the high index is due to a short humerus rather than to a long radius as in brachiating primates. This further illustrates how the forelimb is relatively short in gray squirrels compared with ceboids.

The hindlimb of *Sciurus carolinensis* presents an interesting situation, as illustrated in Table 10. The crural index (tibia/femur) is higher in *Sciurus* than in *Saguinus*. The standardized mean vectors show that this results from both a relatively longer tibia and a relatively shorter femur in gray squirrels compared with tamarins. However, the tibia is negatively allometric to the femur in *Sciurus* and not in *Saguinus*. These facts suggest that if gray squirrels were as big as tamarins, their crural ratios would not be as different.

The data on the lengths and widths of long bones were mentioned earlier. In the total sample of young to fully adult squirrels, the mid-shaft diameters were allometric to the lengths of the long bones and increased at approximately the hypothesized 1.5 power of the latter. The widths of the proximal and distal ends of the humerus and femur clearly were not. (The tibia is assisted by the fibula in transmitting weight from the femur to the foot; therefore, the power function of tibial width to length may be hypothesized to be different than 1.5.) The sample of adult measurements suggests that the hypothesized power relationship does not accurately describe the relationships between distal widths and lengths of humeri and femora. The sample size is small, however, and the significance limits correspondingly broad. The analysis clearly demonstrates how an analysis of robustness of long bones can be biased by inclusion of lengths and widths of bones with unfused growth sutures. It also demonstrates that different widths are best described by different power functions of length measurements. Robustness would appear to be a more complex characteristic than the analyses of Jolicoeur (1963) and Goldstein (1972) indicate.

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